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CONTRIBUTIONS TO THE KNOWLEDGE OF THE DIAPHRAGMS OF WATER PLANTS

I. SCIRPUS VALIDUS

LAETITIA M. SNOW

(WITH SIXTEEN FIGURES)

I. Introduction

The form and structure of water plants have been studied by botanists for many years and much has been written on the subject. Many of these investigators, however, have not mentioned the presence or absence of diaphragms in the plants which they have studied, and the reports of those who have considered these structures are often contradictory. The aim of the present paper is to organize these numerous and conflicting reports and to present certain results, which have been obtained chiefly from a study of *Scirpus validus* Vahl. The other forms which have been studied will be referred to as occasion demands. The work has been carried on at Wellesley College and Wood's Hole.

II. Definition of the term "diaphragm"

LEITGEB (18) evidently considers a diaphragm as any partition which breaks the continuity of the air passage, for he speaks of them as being present at the nodes of *Hippuris*. DUVAL-JOUVE (7), DEBARY (6), and SCHENCK (29) deny the presence of diaphragms in *Hippuris*, but GOEBEL (13) uses this form as an example of a water plant with diaphragms. MEYEN (20) states that the hollow stems of the umbellifers and grasses have no cross-walls, but are interrupted at the nodes by masses of tissue. COURCHET (4), however, considers that diaphragms are present at the nodes of the umbellifers, and HACKEL (11*c*) mentions diaphragms of thick tissue at the nodes of grasses. MEYEN (20, 21) states that the canals in the leaves of *Ceratophyllum* and in the stem of *Myriophyllum spicatum* end blindly in thick tissue. According to DUVAL-JOUVE (7) no diaphragms are found in *Myriophyllum verticillatum*, but they are present in the leaves of *Ceratophyllum;* while DEBARY (6) denies their presence in both genera.

It is evident, therefore, that some writers consider as diaphragms the thick masses of parenchyma at the nodes of certain plants, while others do not. The loose use of the word has led to much confusion, and it is necessary to define the term. The word "diaphragm" should be reserved for the perforated structures, one to several layers thick, which cross at intervals the air passages of plants. This definition excludes from consideration the woody partitions occurring in the pith of certain trees (*Juglans*, etc.), because they are not only relatively massive, but have been proved by WIESNER and MOLISCH (36) to be impervious to air. Owing to the uncertainty as to the exact meaning of the term, unless perforated diaphragms are distinctly mentioned, one can never be sure that such structures are present in the plant under consideration. In the discussion of the distribution of diaphragms among plants, no effort has been made to distinguish the reports of "perforated diaphragms" from those of "partitions," because many references to diaphragms are without descriptions or figures.

III. Occurrence of diaphragms

A. DISTRIBUTION IN THE VARIOUS PLANT GROUPS

From a study of the outline given under the heading above (see p. 514), it is evident that among the angiosperms the great majority of families in which diaphragms have been found are monocotyledons. It cannot be said, however, that they are restricted to this class, or that they are characteristic of certain genera. I have examined representatives of various families of dicotyledons with the result that diaphragms were found in one species only, *Myriophyllum tenellum.* In this species beautiful perforated diaphragms are present at the nodes, while a second species, *Myriophyllum humile,* and a specimen believed to be another species of the same genus show masses of tissue at these points. Further investigations along this line are in progress.

B. IN PLANT PARTS

Diaphragms have been reported for all parts of plants except flowers and fruits, and in the following order as to abundance:

leaves (especially the blade), upright stems, flower stalks, roots, and rhizomes. Only three instances of the presence of perforated diaphragms in roots have been reported: *Enhalus acoroides* (CUNNINGTON 5), *Hydrocharis morsus-ranae* (SAUVAGEAU 23), and *Limnobium Boscii* (MONTESANTO 22). It is possible, however, that the partitions noted in the roots of *Eriocaulon* and a few species of *Paepalanthus* by HACKEL (11*c*) may prove to be true diaphragms. Only one reference (DUVAL-JOUVE 7) has been made to the presence of diaphragms in rhizomes.

C. UNDER VARYING CONDITIONS OF SOIL MOISTURE

LEITGEB (18) states that diaphragms are found "especially in leaves of swamp and water plants." DUVAL-JOUVE (10), in his study of partly submerged grasses, found air spaces and diaphragms present in the immersed parts only. SOLEREDER (32), on the other hand, reports their presence in the aerial as well as the submerged parts of the leaves of *Stratiotes*. DUVAL-JOUVE (9) found no diaphragms in the leaves of *Iris germanica* growing in a dry habitat, but found them in *I. pseudacorus* and *I. foetidissima* growing in water or wet places. He did not, however, test the same species in the two habitats.

My work upon *Scirpus validus* has shown no apparent difference, as to the presence or structure of diaphragms, between the immersed and the aerial parts. Experiments are at present in progress to test the possibility of growing this species in drained soil, and to investigate any structural changes which may take place under drier conditions.

IV. Structure

A. OF DIAPHRAGMS

In accordance with the reports for various plants, the diaphragms of *Scirpus validus* are one to several layers thick. Commonly in old stems the greater extent of the diaphragm is composed of one layer of cells, which increases to several layers around the cross-bundle (fig. 7). As a rule, a diaphragm extends over one air space, but DUVAL-JOUVE (9) states that those of *Cyperus Papyrus*, *Thalia dealbata*, *Butomus umbellatus*, and *Sagittaria* *lancifolia* may extend over several spaces; and SCHWENDENER (30) finds the same to be true for *Papyrus antiquorum*. Only in rare instances do the diaphragms of *S. validus* extend over more than one space.

The shape of the cells varies, with the species studied, from polygonal cells with tiny air spaces at the corners, to stellate cells with very much elongated arms. A study of *S. validus*, taken in connection with the reports of DUVAL-JOUVE (9) for *S. lacustris*, *S. littoralis*, and *S. triquetrii*, and of DEBARY (6) and MEYEN (21) for *S. lacustris*, suggests "scirpus type" as an appropriate term by which to designate diaphragms showing the peculiar arrangement of cells characteristic of these species. In this type the cells are elongated and have very short arms. These long narrow cells occur in groups of two, three, four, or five, the usual number being four. While the cells in a single group are all elongated in the same direction, the different groups (with certain exceptions to be noted later) have their axes of elongation pointing in different directions. DUVAL-JOUVE (9) states that *Sagittaria lancifolia* has this type of diaphragm, except that the cells are in groups of two (his figure, however, does not agree with the statement), and that *S. sagittifolia* and *Alisma Plantago* resemble *S. lancifolia*. In another paper (10) he states that the diaphragms in "certain species of grasses" have cells in groups of four. A study (as yet incomplete) of the different species of *Scirpus* leads to the conclusion that some species of the genus may possess more than one type of diaphragm. It has not yet been determined whether any correlation

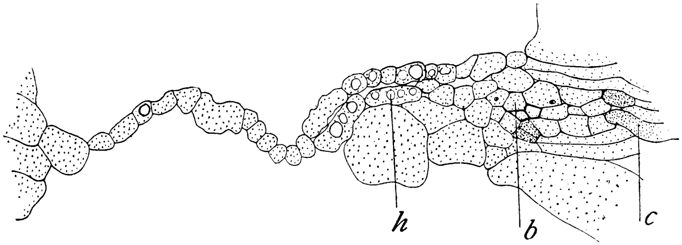

FIG. 1.—Flax seedling: longitudinal section through hypocotyl: *c*, ordinary cortical cells; cells are elongating in the direction of food current passing to meristem beyond *h*; *b*, young bundle; ×110.

exists between the different types of diaphragm and the presence or absence of cross-bundles.

Although both vascular and non-vascular diaphragms are mentioned by writers, the former so far outnumber the latter that some authorities consider the chief function of diaphragms to be the support of the cross-bundles. In *Scirpus validus* the presence of cross-bundles is so nearly universal that the relatively few instances where they cannot be found lead one to suspect that in these cases the material has been broken or a section or two lost at the critical point.

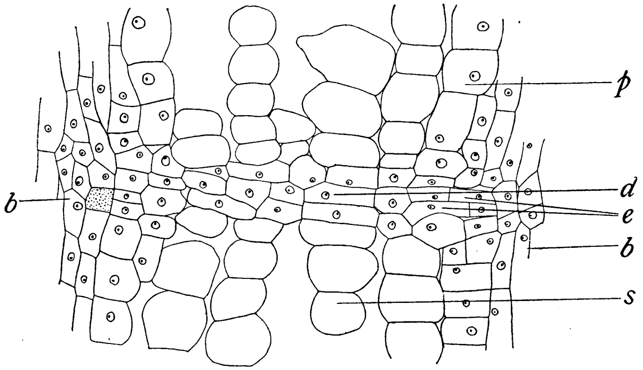

FIG. 2.—*Scirpus validus:* longitudinal section of very young stem: diaphragm cells elongating to form cross-bundle; nuclei indicate the greater density of protoplasmic contents of cells of diaphragm and partition walls of spaces; some nuclei were not demonstrable but were placed arbitrarily; *p*, partition cells; *d*, diaphragm cells; *b*, young longitudinal bundle; *s*, cells of space; *e*, elongating cells; ×175.

B. OF CROSS-BUNDLES

DUVAL-JOUVE (9) describes the cross-bundles of *Musa paradisiaca* as containing large spiral vessels; those of *Butomus umbellatus*, *Alisma Plantago*, *Sagittaria lancifolia*, and *S. sagittifolia* as bundles of tracheae. He states in one report (8) that the cross-bundles connect with the outer part of the longitudinal bundles. In his next paper (9) he describes a cross-bundle as articulating itself with the side of the longitudinal bundle, a little back of the large vessels and opposite the interior region of tracheids and small vessels. A figure in a third paper (10) shows a cross-bundle uniting with the phloem.

A study of the cross-bundles of *Scirpus validus* leads to the conclusion that both conditions occur, and are dependent upon the age of the diaphragm. In the very young stem the cells of the cross-bundle are similar to those of the diaphragm and connect with the phloem (figs. 2 and 12). Later the cells greatly elongate, some of those in the center of the bundle become transformed into tracheids with very indistinct spiral (?) markings, and a secondary connection with the xylem of the longitudinal bundle is established (figs. 3 and 4).

DUVAL-JOUVE (9) mentions the fact that in *Sagittaria lancifolia* the bundles do not run on the diaphragms but in them, thus implying that the reverse is usually the case. The diaphragms of *Scirpus validus* run in the diaphragms, as is shown in fig. 5.

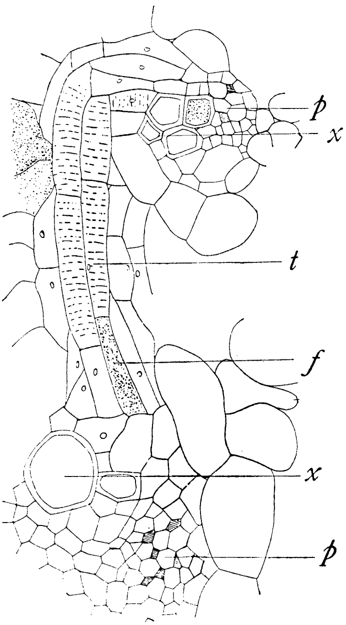

FIG. 3.—*Scirpus validus:* cross-section of stem: two longitudinal bundles connected by a cross-bundle; connection originally with phloem (*p*); tracheids (*t*) have formed and made secondary connection with xylem (*x*); the connection is not yet established with larger bundle; this bundle lies near the edge of a space, but is not connected with a diaphragm; *f*, food storage cells; ×175.

V. Origin

A. OF THE STELLATE PARENCHYMA

The canals of many water plants are filled with a network of stellate cells. In the case of *Scirpus validus* the cells on the upper and lower surfaces of the diaphragms connect directly with these stellate cells, and in some places have been seen to grade into them. It is necessary, therefore, to inquire into the origin of the stellate tissue.

SCHACHT (28) states that the arms of the stellate cells are caused by greater growth, due to a greater amount of nourishment, at certain points. LEITGEB (18) discusses the development of this tissue at some length, and considers the star-shape to be a result of adhesion at certain points, combined with the growth of the surrounding tissue and the "pressure of the secreted air." That the growth of the surrounding tissue causes a pulling out of the cell is indicated by the "diminishing cell body." He adds that the arms, after having been formed, increase in size (presumably by growth). DUVAL-JOUVE (7) considers that the body of the cell does not increase in size, but that the arms grow out as rays; the presence of apparently bifurcated rays indicates a pulling out of the body. In another paper (10) he speaks of the pulling out of the cells from the points of contact. SCHWENDENER (30) believes stellate cells to be due, not directly to a pull, but to growth under a tension caused by the faster growth of the surrounding tissue. DEBARY (6) speaks of cells growing into long arms. LE BLANC (17) gives the same explanation as LEITGEB (whose paper he has apparently not seen), and proves the existence of tension in stellate tissue by an experiment. By bursting one of the stellate cells in a diaphragm, he found that a round hole resulted, which was larger than the original cell, and which was caused by a retraction of the surrounding cells.

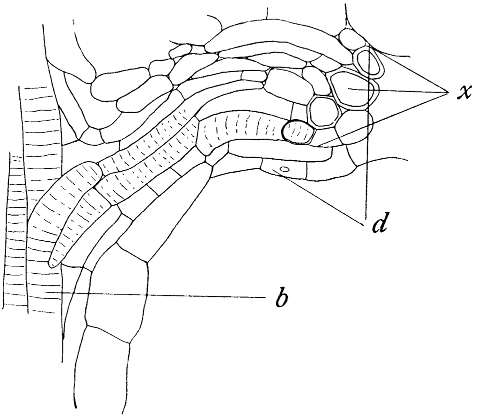

FIG. 4.—*Scirpus validus:* longitudinal section of stem: cross-bundle curving, part in cross-section (*x*) and part in longitudinal section; xylem making connection with xylem of longitudinal bundle (*b*); ×175.

LEITGEB (18) does not explain the formation of the intercellular spaces otherwise than by the pressure of the secreted air. TSCHIRCH (34) thinks that intercellular spaces are formed by a splitting of the primary membrane, because the spaces are covered with a substance giving the same reaction as the primary membrane. GOEBEL

(13), in his study of aerenchyma, came to the conclusion that the cells adhere by the thickenings of the walls, while the pits remain free. MANGIN (19) believes the split to be due to a gelatinization of pectates in the wall, which substances, in consequence, line the intercellular space thus formed.

A study of the stellate parenchyma of *Juncus effusus* leads me to the conclusion that SCHWENDENER has given the correct explanation of the origin of this type of cells. All cells pass through a curve of growth. The center is the oldest part of the pith and reaches the mode of the curve first. As the growth in this region becomes slower, the outer parts are approaching the mode of the curve. Thus the growth of the central cells cannot keep pace with the growth of the outer cells and they are, in consequence, pulled out into arms. The slower the growth the greater the proportion of pull, and consequently very old cells have quite long, slender arms. By taking an average of the longest and the shortest diameters of the bodies of many pith cells at the same stage of development, and comparing it with similar averages for pith cells at different stages, it was found that the cell body passed from 25.6 μ at the tip of the stem, to 21.5 μ a little farther back, and to 17.1 μ still farther back. In any one section the cells at the center are at a much later stage of development than those toward the outside of the stem (fig. 16).

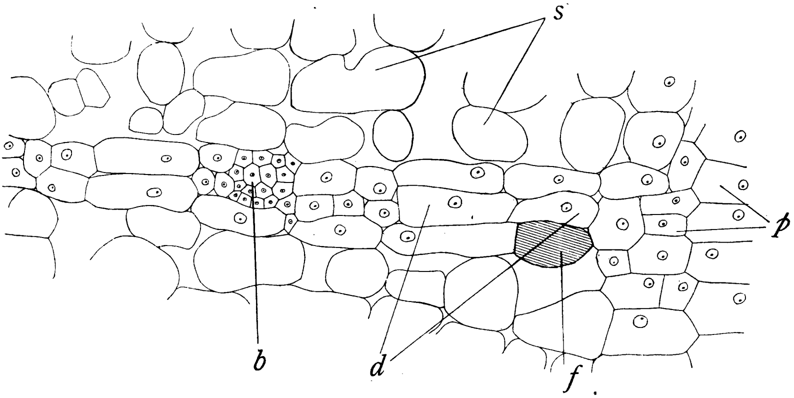

FIG. 5.—*Scirpus validus:* longitudinal section of young stem: diaphragm with cross-section of cross-bundle; nuclei as in fig. 2; *s*, cells of space; *p*, partition cells; *b*, cross-bundle; *d*, ordinary diaphragm cells; *f*, food storage cells; ×175.

B. OF DIAPHRAGMS

LEITGEB (**18**) states that he cannot account for the fact that some cells do not pull out, but remain as diaphragms. MEYEN (**21**), studying *Scirpus lacustris*, and FALKENBERG (**12**), studying *Typha* leaves, state that diaphragms result from stellate parenchyma by a separation of this tissue into layers. CUNNINGTON (**5**) finds that the diaphragms in the leaves of *Enhalus acoroides* arise from small cells cut off from the original mesophyll cells. These small cells increase in one plane and form plates separating the other mesophyll cells, which elongate in a plane perpendicular to these plates and thus separate them by spaces.

In *Scirpus validus* there are no special cells which give rise to diaphragms. In *Juncus effusus* the parenchyma splits into layers which retain an occasional vertical connection (fig. 15). In longitudinal sections of *Scirpus* a similar layering may be observed. The cells of some of the layers retain their meristematic character and continue to divide and to keep pace with the growth of the surrounding tissues, thus forming diaphragms. The other cells become stellate by the process already described (figs. 2, 5, 12, 13).

C. OF THE GROUPS OF CELLS IN THE DIAPHRAGMS

Several writers have noted or figured the diaphragm cells in groups of four. DUVAL-JOUVE (**9**) reports this arrangement for several species of plants, but offers no explanation as to the origin of the groups. DEBARY (**6**) believes each group of cells in the diaphragms of *Scirpus lacustris* to originate from one mother cell.

From a comparison of figs. 12 and 13, it seems evident that such an origin as that suggested by DEBARY is reasonably probable. The number, however, is not invariably four, but groups of three and five also appear (fig. 6). The reason for the formation of two, three, or four walls parallel to the long axis of the cell is not easily explained in terms of cytological mechanics. It was suggested to me that a study of the adventitious buds of flax seedlings might throw light upon the subject. Flax seedlings were grown, therefore, until the cotyledons had opened, and were then decapitated. After about a week or ten days small swellings (adventitious buds) appeared on the hypocotyl. It is found, upon studying longitudinal sections of these hypocotyls, that the meristem of the bud is composed of small cubical cells which have arisen, by division, from the epidermis and outer cortical cells. Deeper cortical cells, however, are found to be elongating and apparently dividing parallel to their long axes, that is, in the direction of the current of food materials passing to the growing meristem (fig. 1).

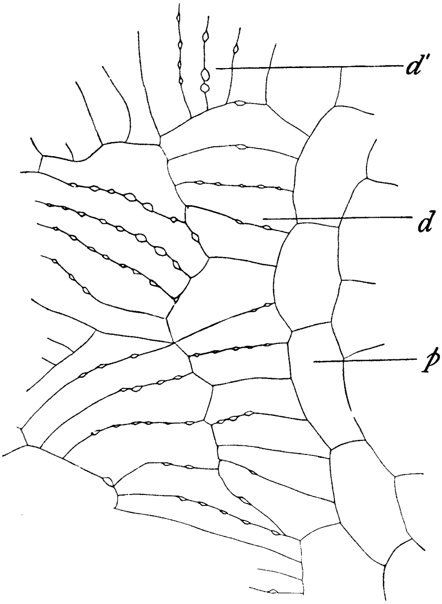

FIG. 6.—*Scirpus validus:* cross-section of older stem: *p*, partition cells; *d*, diaphragm cells perpendicular to the partition; *d′*, cells not in position characteristic of cells adjoining partitions; ×175.

It is well known that HABERLANDT (**15**) correlates the shape of the palisade cells with the transportation of the products of photosynthesis. A similar elongation of cells for the purpose of conduction is found in the secondary transfusion tissue of *Cycas*, where, according to WORSDELL (**38**), the ordinary mesophyll cells become modified in order to supply water to the parts of the leaf which are distant from the bundle. From GOEBEL'S study of adventitious buds (**14**) it is seen that the bundle becomes differentiated first in the leaf and afterward extends itself backward, until it reaches and becomes connected with a bundle in the stem. This elongation of cells to continue the bundle may be interpreted as a result of the current of food materials passing to and from the growing leaf. In a similar way the current of food materials from the cross-bundle to the partition walls of the air space may determine the direction of the walls of the groups of cells in the diaphragms.

VI. Function of diaphragms

A. MECHANICAL

1. *To resist strain.*—SCHWENDENER (30) considers diaphragms to be girders; HABERLANDT (15) and LE BLANC (17) agree with him, but believe strengthening to be only one of their functions. This is probably true. If certain species of *Juncus* with nodose stems and leaves be compared, it will be seen that those forms having firm, stiff outer walls have a smaller number of cross-partitions than have those with softer walls.

2. *Support of cross-bundles.*—LEITGEB (18), DUVAL-JOUVE (9), DEBARY (6), and SAUVAGEAU (25) definitely state that diaphragms are for the support of cross-bundles. LE BLANC (17) assigns it as one of their functions. Where cross-bundles occur there can be no doubt as to the value of such support. It cannot be assigned as a function of all diaphragms, however, because non-vascular diaphragms appear to be characteristic of certain plants.

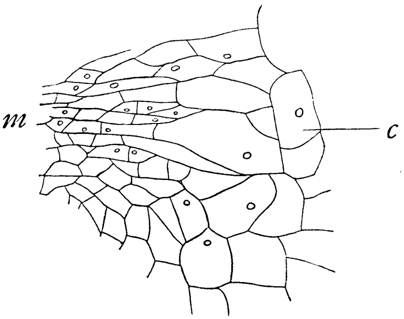

FIG. 7.—*Scirpus validus:* longitudinal section of stem: diaphragm varying in thickness; cross-bundle (*m*) at edge of diaphragm establishing connection with a longitudinal bundle beyond section; cells stippled to distinguish from spaces; *c*, cut arms of cells; ×110.

B. TO PREVENT THE ENTRANCE OF WATER

GOEBEL (13) believes that diaphragms are of use in keeping water from entering broken parts, stating that it takes great pressure to infiltrate the air passages. It is quite probable that the small size of the perforations in the diaphragms prevents the entrance of water against the pressure of the contained air. The fact that, in order to force killing fluids into the tissues of plants with diaphragms or with small intercellular spaces, it is necessary to exhaust the air with a pump indicates the difficulty with which water penetrates small openings against air pressure. This difficulty might be increased by the presence of cutin on the walls of the diaphragm cells, but the walls of these cells in *Scirpus validus* give the cellulose reaction only.

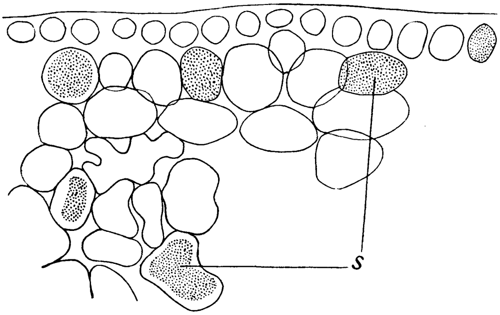

FIG. 8.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: epidermis, parenchyma, and spongy tissue of air space shown; section treated with Fehling's solution; strong reaction indicated by stippling (*s*); merely size, position, and shape of cells indicated; ×175.

SAUVAGEAU (27) found that after injecting the stem with water, some of the canals were suberized, and concluded that suberization takes place after contact with water, to prevent infiltration of the surrounding tissues. As he offers no direct proof of suberization following contact with water, definite conclusions cannot be derived from this work.

C. TO AID IN CIRCULATION OF AIR

HABERLANDT (15) and LE BLANC (17) include this among the functions of diaphragms. It seems evident that, given partitions, it is advantageous to have them perforated, to allow circulation of air. The statement made by GOEBEL (13) that nonperforated diaphragms in *Pontederia crassipes* (*Eichhornia*) allow circulation of air needs proof.

D. NUTRITION

LE BLANC (17) supports CHATIN[1] in believing nutrition to be one of

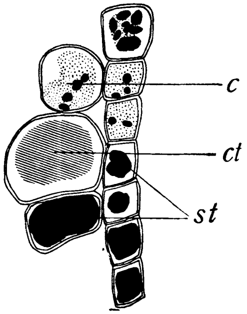

FIG. 9.—*Scirpus validus:* a few cells from cross-section of leaf of young bud: treated with Fehling's solution, I in KI, and $K_2Cr_2O_7$; *c*, cell showing cytoplasm and scattered starch grains; *ct*, cell with contents plasmolyzed, starch grains not distinguishable; *st*, cell which has reduced Fehling's solution and given tannin test with $K_2Cr_2O_7$; ×175.

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[1] CHATIN, ADOLPHE, Anatomie comparée des végéteaux. Paris. 1856–1862. I have not been able to obtain this publication.

the functions of diaphragms. Food manufacture undoubtedly takes place, to some extent, in very young diaphragms of *Scirpus validus* which are close to the exterior. As the stem grows larger and the diaphragms are removed from the exterior by the growth of the outer tissues, they lose their chlorophyll and appear glistening white.

E. STORAGE

That food (or waste) is stored in diaphragm cells is evident at a glance (figs. 12 and 13), but the nature of the stored material has not been definitely determined. SAUVAGEAU (**24–27**) notes secretory cells in various forms of water plants, and in certain places definitely calls the contents tannin. SOLEREDER (**31**) records the presence of tannin-bearing cells in the diaphragms and the walls of air spaces of the Hydrocharitaceae. He tested with vanillin and concentrated hydrochloric acid, as suggested by HARTWICH and WINCKEL (**16**), and obtained the phloroglucin reaction. He obtained the same result with HCl alone, which showed that an aldehyde, similar in action to vanillin, was present. He found in *Vallisneria* that the contents of certain cells gave the tannin reaction with iron, while other cells were filled with a clear oil-like material.

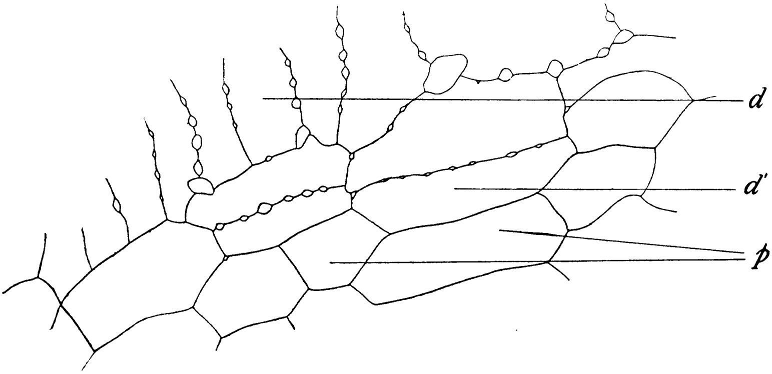

FIG. 10.—*Scirpus validus:* cross-section of stem at edge of diaphragm: *d*, diaphragm cells in position characteristic for cells adjoining a partition; *d'*, cells of partition which have assumed the character of diaphragm cells and are therefore not in the characteristic position; *p*, partition cells; ×175.

In material of *Scirpus validus* killed with chromacetic acid, many brown storage cells appear. An investigation of the chemical nature of the storage material led to the following results. Fresh sections after having been boiled in Fehling's solution showed many red-brown cells (fig. 8). The sections were then washed in water and treated with a solution of iodine in potassium iodide. These "sugar cells" remained red-brown, while the others gave a strong starch reaction. The sections were again washed in water and then treated with potassium bichromate, and the reddish cells turned very dark brown. Fig. 9 shows a portion of a section at this stage. Tested with ferric chloride these "sugar cells" gave the characteristic tannin reaction. Trimble (**33**) states that glucose is frequently present with tannin, and also that tannin will reduce Fehling's solution; consequently the reactions described above may be due to tannin and glucose or to tannin alone. Trimble also found that in the rhizome of *Acorus Calamus*, the tannin-bearing cells were quite distinct from the starch-bearing cells.

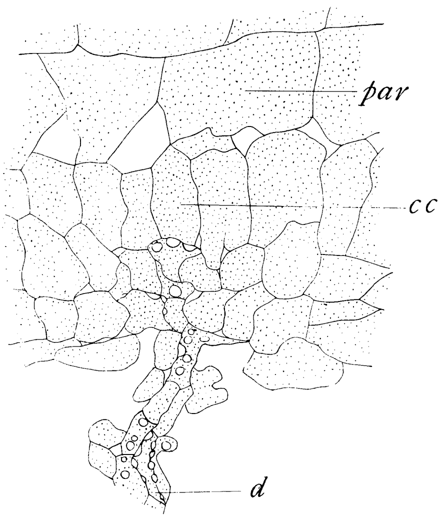

Fig. 11.—*Scirpus validus:* longitudinal section of stem: *d*, diaphragm extending into partition; *par*, ordinary, polygonal, partition cells; *cc*, partition cells elongated for conductive function; circles in cells indicate cut arms; stippling to distinguish cells from spaces; ×110.

When fresh specimens of *Scirpus validus* were tested with vanillin and concentrated HCl, according to the method described by Hartwich and Winckel (**16**), it was found that numerous cells turned ruby red. This reaction showed the presence of phloroglucin or some related tannoid. The reaction did not take place with HCl alone, therefore the necessary aldehyde was not present in the cells. Washing the sections in water caused the red color to disappear, and subsequent treatment with $K_2Cr_2O_7$ brought out strongly the tannin reaction. This took place at once, instead of slowly, as before the phloroglucin test.

To ascertain if gallic acid was present, fresh sections were treated with potassium cyanide (TRIMBLE 33). The majority of the sections gave no reaction, but one or two showed a faint diffuse pinkish tint at one corner where there was a mass of very dark brown sclerenchyma cells. Left over night, many cells turned a very pale brown, thus showing the presence of tannin rather than gallic acid. When the sections, which had been washed after the phloroglucin test, were treated with KCN, many cells (presumably those which had responded to the previous test) immediately turned dark brown. It is thus seen that after the phloroglucin test the tannin reaction takes place with great rapidity and clearness.

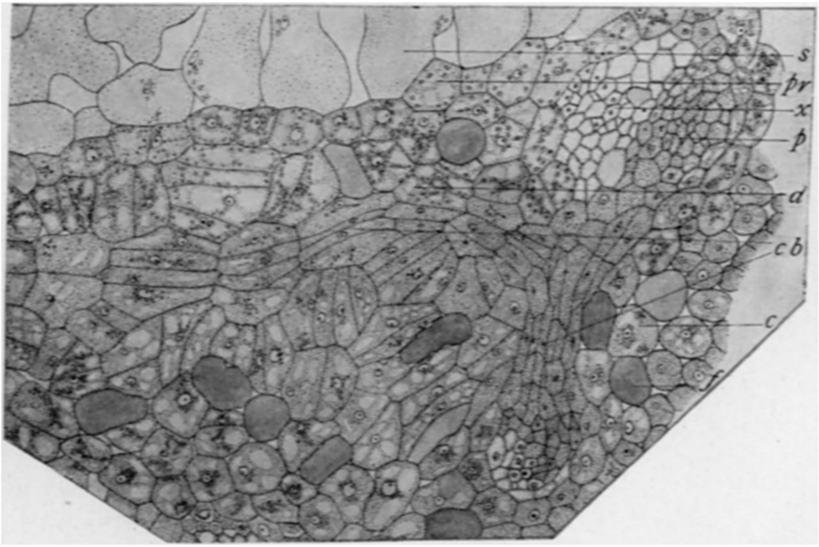

FIG. 12.—*Scirpus validus:* cross-section of tip of very young stem: two longitudinal bundles and connecting cross-bundles (*cb*); the latter runs in a diaphragm (*d*); cross-bundles connect with phloem (*p*); diaphragm cells starting to form groups; note similarity between cells of diaphragm and of cross-bundles; *c*, cortical parenchyma; *pr*, partition wall separating two spaces; *s*, cells of space; *x*, xylem; *f*, food storage cells; ×175.

Since the fresh cells give the tannin reaction with $K_2Cr_2O_7$ and $FeCl_3$, and also the phloroglucin reaction, it is possible that the food is stored as some tannin compound containing the phloroglucin radical. I am not sufficiently familiar with the chemistry of the tannin compounds to make any further suggestions as to the nature of the stored material.

Storage cells are very abundant in the diaphragms and in the parenchyma of the stems of *Scirpus validus*, but are also present in the scales of young buds, the spongy parenchyma of the rhizome, and in both longitudinal and cross-bundles. They have not been observed in the young roots of this species.

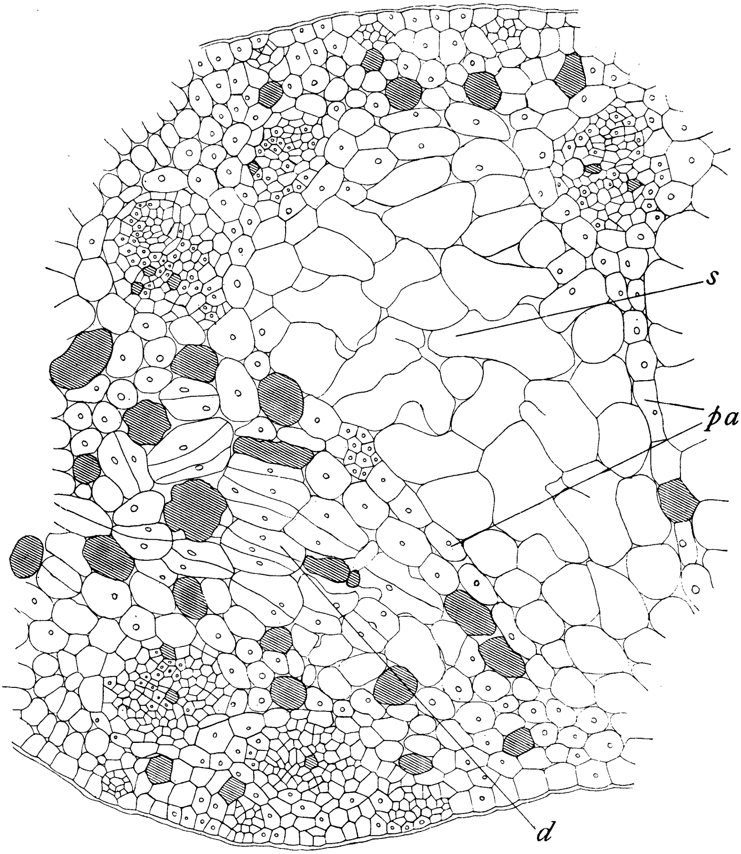

FIG. 13.—*Scirpus validus:* cross-section of tip of very young stem: *par*, partitions separating three spaces; *s*, cells of space which will become stellate; *d*, young diaphragm; note great number of food storage cells in diaphragm; ×110.

F. CONDUCTION

To the above-mentioned functions may be added that of conduction. An examination of figs. 6, 10, and 12 will show that the groups of cells adjoining the cross-bundle and the partition walls of the air spaces have their long axes perpendicular to the bundle and the walls respectively. This is an almost universal condition; where

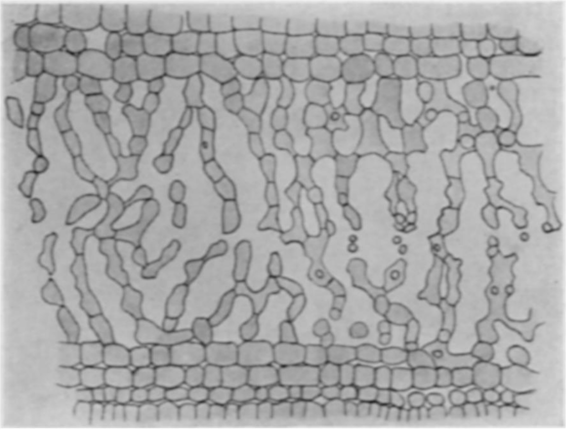

FIG. 14.—*Juncus effusus:* a few cells from cross-section of stem, showing transition from rounded cells on outer edge of pith to stellate cells nearer the center; ×110.

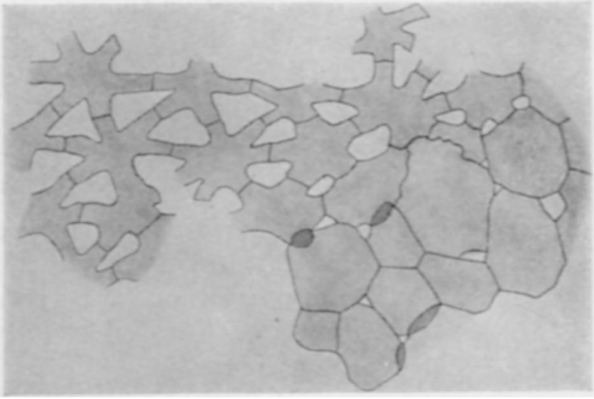

FIG. 15.—*Juncus effusus solutus:* longitudinal section of stem showing formation of cross-layers in stellate parenchyma; ×35.

there are exceptions, some at least can be shown to be partition cells which have secondarily assumed the character of diaphragm cells (fig. 10). Around storage cells the diaphragm cells frequently assume a rosette arrangement (fig. 16), apparently for conductive purposes. The fact that the first connection of the cross-bundle with the longitudinal bundle is with the phloem also lends weight to this suggestion. Longitudinal sections show that the diaphragm cells extend a short distance into the partitions, and that the ordinary polygonal partition cells become elongated and slope toward the diaphragm, thus suggesting a conductive function (fig. 11). From these conditions it seems reasonable to conclude that conduction is one function of the diaphragms of *Scirpus validus*.

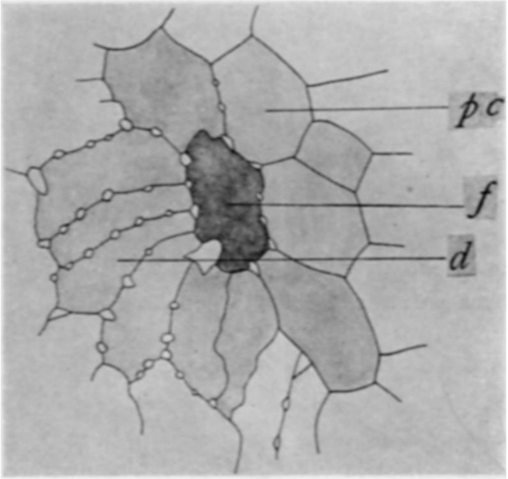

FIG. 16.—*Scirpus validus:* a few cells at edge of diaphragm: *f*, food storage cell; *d*, diaphragm cells leading to or from storage cell; *pc*, cortical parenchyma; ×175.

Summary

1. Diaphragms, although present in many monocotyledons, are not restricted to that group. The present state of our knowledge, however, does not allow us to make definite statements as to their distribution.

2. Diaphragms are especially characteristic of leaves, but have been reported for all parts of plants except flowers and fruits.

3. Diaphragms have been found in immersed and in aerial parts of plants.

4. Diaphragms appear to be characteristic of plants growing in water or very wet places.

5. The structure of diaphragms varies: (*a*) they may be one to several layers thick; (*b*) the cells vary from polygonal to stellate; in the "scirpus type" the cells are in groups (usually of four) and are long and narrow, with short arms; (*c*) the presence of cross-bundles appears to vary with the form studied. In *Scirpus validus* nearly all the diaphragms have bundles in them.

6. The cross-bundle is made up of xylem and phloem. At first the connection with the longitudinal bundles is with the phloem, but later a secondary connection is made with the xylem.

7. The stellate cells originate from ordinary parenchyma cells by the differential growth of the cells from the inside outward.

8. Diaphragms in *Scirpus validus* arise by a division of the parenchyma into layers, some of which retain their meristematic character, while the remaining cells gradually cease growing and become the slender stellate cells of the air spaces.

9. Each group of four cells of the diaphragm of *Scirpus* spp. arises from a mother cell. The formation of dividing walls parallel to the long axes of the cells is probably determined by the current of food materials passing from the cross-bundle to the partition walls of the space.

10. Diaphragms have the following functions: (*a*) to resist strains and keep the spaces open; (*b*) to support cross-bundles; (*c*) to prevent entrance of water by the small size of the perforation; (*d*) perforations permit air to circulate; (*e*) while young and green, to manufacture carbohydrates; (*f*) to store food: (i) this is possibly in the form of some tannin compound containing the phloroglucin radical, and may or may not be associated with glucose; (ii) this substance is stored in special cells which are distinct from the starch-bearing cells; (*g*) to conduct food materials from the cross-bundle to the partition walls of the space.

My thanks are due Professor KARL M. WIEGAND for his kindly assistance in the identification of the species studied, and

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WELLESLEY COLLEGE

THE DISTRIBUTION OF DIAPHRAGMS IN THE VARIOUS GROUPS OF PLANTS

1. PTERIDOPHYTES.—They are reported for ferns and *Equisetum* by LEITGEB (18), but are not mentioned by COSTANTIN (3) in his report on *Equisetum*.

2. SPERMATOPHYTES.—

a) No mention has been made of the presence of diaphragms in the gymnosperms.

b) Diaphragms have been observed in the following families of angiosperms:

(1) *Dicotyledons:*

In Nymphaeaceae by LEITGEB (18), SOLEREDER (31), and LE BLANC (17). Their presence in *Nelumbium* (*Nelumbo*) is denied by DEBARY (6).

In Ceratophyllaceae by DUVAL-JOUVE (7), but their presence is denied by MEYEN (20, 21), DEBARY (6), and SCHENCK (29).

In Haloragidaceae by LEITGEB (18) and GOEBEL (13), but their presence is denied by MEYEN (20, 21), DUVAL-JOUVE (7), DEBARY (6), and SCHENCK (29).

In Gentianaceae by DUVAL-JOUVE (9), but their presence in *Limnanthemum nymphoides* is denied by DEBARY (6).

In Rubiaceae by UNGER (35) for *Richardia aethiopica* (authority not noted). In ENGLER and PRANTL *Richardsonia* is given as a synonym for *Richardia*, but the species *aethiopica* does not appear, and it is not safe to conclude from this report that diaphragms occur in this family.

In Umbelliferae by LEITGEB (18) and (at nodes) by COURCHET (4), but their presence is denied by MEYEN (20).

In Compositae by LEITGEB (18).

COSTANTIN (3) made an extended study of water plants, including many families, the greater number of which were dicotyledons, but he does not mention the presence of diaphragms. LE BLANC (17) states that they occur only in monocotyledons and the related Nymphaeaceae.

(2) *Monocotyledons:*

In Typhaceae by LEITGEB (18), DUVAL-JOUVE (7, 9), and FALKENBERG (12).

In Pandanaceae by MEYEN (20).

In Sparganiaceae by DUVAL-JOUVE (7, 9).

In Potamogetonaceae by DUVAL-JOUVE (9), SAUVAGEAU (25, 26, 27), and MEYEN (21). Their presence is denied in *Zostera* and *Posidonia caulini* by DEBARY (6). SAUVAGEAU (25) reports them for *Zostera*, but does not consider the thin partitions extending from epidermis to epidermis in the leaves of *Posidonia caulini* and *Cymodocea antarctica* to be diaphragms. He does not mention diaphragms in his reports on *Phyllospadix* (26) and *Ruppia* (27).

In Najadaceae by LEITGEB (18).

In Hydrocharitaceae by MEYEN (20), SAUVAGEAU (23, 24, 25), SOLEREDER (32), MONTESANTOS (22), and CUNNINGTON (5). BALFOUR (1) states that the canals of *Halophila* end at the nodes in thick tissue, and CASPARY (2) makes the same statement for the Hydrilleae. SAUVAGEAU (24) does not mention diaphragms in his report on *Halophila*.

In Aponogetonaceae by DUVAL-JOUVE (9) and in ENGLER and PRANTL (11*c*).

In Juncaginaceae in ENGLER and PRANTL (11*c*).

In Alismaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (9), and MEYEN (20).

In Butomaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9). No mention of diaphragms is made by COSTANTIN (3) in his report on *Butomus*.

In Gramineae by LEITGEB (18), DUVAL-JOUVE (7, 8, 9, 10), and MEYEN (20).

In Cyperaceae in ENGLER and PRANTL (11*c*), by MEYEN (20, 21), LEITGEB (18), DUVAL-JOUVE (7, 9), SCHWENDENER (30), FALKENBERG (12), and DE-BARY (6).

In Araceae by MEYEN (21), LEITGEB (18), DUVAL-JOUVE (9), and WEISS (37).

In Eriocaulaceae (?) in ENGLER and PRANTL (11*c*).

In Mayacaceae. The description of the leaves in ENGLER and PRANTL (11*c*) suggests the presence of diaphragms.

In Pontederiaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), DUVAL-JOUVE (7, 9), and GOEBEL (13).

In Juncaceae in ENGLER and PRANTL (11*c*), by DUVAL-JOUVE (7, 8, 9), and SCHWENDENER (30).

In Liliaceae by MEYEN (20) and DUVAL-JOUVE (9).

In Iridaceae by DUVAL-JOUVE (9).

In Musaceae in ENGLER and PRANTL (11*c*), by MEYEN (20), and DUVAL-JOUVE (9).

In Cannaceae by MEYEN (20) and LEITGEB (18).

In Marantaceae in ENGLER and PRANTL (11*c*) and by DUVAL-JOUVE (9).

LITERATURE CITED

1. BALFOUR, BAYLEY, On the genus *Halophila*. Trans. Bot. Soc. Edinburgh 13:290–343. *pls. 8–12*. 1879.
2. CASPARY, ROBERT, Die Hydrilleen (Anacharideen Engl.). Jahrb. Wiss. Bot. 1:377–513. *pls. 35–39*. 1858.
3. COSTANTIN, J., Recherches sur la structure de la tige des plantes aquatiques. Ann. Sci. Nat. Bot. VI. 19:287–331. *pls. 14–17*. 1884.

4. Courchet, M., Étude anatomique sur les Umbellifères et sur les principales anomalies de structure que présentent leurs organes végétatifs. Ann. Sci. Nat. Bot. VI. **17**:107–128. *pls. 10–12.* 1884.

5. Cunnington, Hilda M., Anatomy of *Enhalus acoroides* (Linn. f.) Zoll. Trans. Linn. Soc. Bot. London **7**:355–371. *pl. 36. figs. 13.* 1912.

6. DeBary, A., Comparative anatomy of phanerogams and ferns. Oxford. 1884.

7. Duval-Jouve, J., Sur quelques tissues de *Juncus* et de Graminées. Bull. Soc. Bot. France **16**:404–410. *pl. 3.* 1869.

8. ———, Same title. Bull. Soc. Bot. France **18**:231–239. *pl. 2.* 1871.

9. ———, Diaphragmes vasculifères des Monocotylédones aquatiques. Mém. Acad. Sci. Montpellier **8**:157–176. *pl. 8.* 1871.

10. ———, Histotaxie des feuilles de Graminées. Ann. Sci. Nat. Bot. VI. **1**:294–371. *pls. 16–19.* 1875.

11. *a*) Engler, A., and Prantl, K., Natürlichen Pflanzenfamilien. Pt. III. **7**:226–237.
    b) ———, *Idem*, Pt. III. **2**:12.
    c) ———, *Idem*, Pt. II. **1**:1–6.

12. Falkenberg, P., Vergleichende Untersuchungen über dem Bau der Vegetationsorganen der Monocotyledonen. Stuttgart. 1876.

13. Goebel, Karl, Pflanzenbiologische Schilderungen. Pt. II. 115–266. 1891.

14. ———, Über Regeneration im Pflanzenreich. Biol. Centralbl. **22**:385–397, 417–438, 481–505. *figs. 1–21.* 1912.

15. Haberlandt, G., Physiologische Pflanzenanatomie. 3d edition. Leipzig. 1904. pp. 246–260, 388–395.

16. Hartwich, C., und Winckel, M., Über das Vorkommen von Phloroglucin in Pflanzen. Arch. Pharmazie **242**:462–475. 1904.

17. Le Blanc, M., Sur les diaphragmes des canaux aérifères des plantes. Rev. Gén. Bot. **24**:233–243. *pl. 10.* 1912.

18. Leitgeb, H., Die Luftwege der Pflanzen. Sitzungsber. Kais. Akad. Wiss. Wien **18**:334–363. *pl. 1.* 1857.

19. Mangin, L., Sur les composés pectiques. Jour. Botanique **7**:329. 1893.

20. Meyen, Franz J. F., Phytotomie. Berlin. 1830. pp. 85, 193–206.

21. ———, Neues System der Pflanzenphysiologie. Berlin. 1837. pp. 294–309.

22. Montesantos, Nikolaus, Morphologische und biologische Untersuchungen über einige Hydrocharideen. Flora **105**:1–32. *pls. 1–5.* 1912.

23. Sauvageau, C., Sur la présence de diaphragmes dans les canaux aérifères de la racine. Compt. Rend. **106**:78–79. 1888.

24. ———, Sur la feuille des Hydrocharidees marines. Jour. Botanique **4**:269, 289, 295. *figs. 3.* 1890.

25. ———, Observations sur la structure des feuilles des plantes aquatiques, *Zostera*, *Posidonia*, *Cymodocea*, etc. Jour. Botanique **4**:41, 68, 117, 129, 173, 181, 221, 237. 1890.

26. Sauvageau, C., Sur la structure de la feuille des genres *Halodule* et *Phyllospadix*. Jour. Botanique **4**:321–332. *figs. 7*. 1890.
27. ———, Sur les feuilles de quelques Monocotylédones aquatiques. Ann. Sci. Nat. Bot. VII. **13**:103–296. *figs. 64*. 1891.
28. Schacht, Hermann, Physiologische Botanik. Die Pflanzenzelle, der innere Bau und das Leben der Gewächse. Berlin. 1852. pp. 70, 166.
29. Schenck, Heinrich, Vergleichende Anatomie der submersen Gewächse. Bibl. Bot. **1**: 1887.
30. Schwendener, S., Das Mechanische Princip im anatomischen Bau der Monocotyledonen. Leipzig. 1874. pp. 89–92.
31. Solereder, Hans, Systematische Anatomie der Dicotyledonen. Stuttgart. 1899.
32. ———, Systematisch-anatomische Untersuchungen des Blattes der Hydrocharitaceen. Beih. Bot. Centralbl. **30**:24–104. *figs. 53*. 1913.
33. Trimble, Henry, The tannins. 1892.
34. Tschirch, A., Angewandte Pflanzenanatomie. Vol. I. Wien u. Leipzig. 1880. pp. 428–431.
35. Unger, Franz, Grundlinien der Anatomie und Physiologie der Pflanzen. Wien. 1866.
36. Wiesner, J., and Molisch, H., Untersuchungen über die Gasbewegung in der Pflanze. Sitzungsber. Kais. Akad. Wiss. Wien **98**:670–713. 1889.
37. Weiss, G. A., Anatomie der Pflanzen. Wien. 1878. pp. 295–306.
38. Worsdell, W. C., On transfusion tissue: its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. London. Bot. II. **5**:301–319. *pls. 23–26*. 1892.